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Variability in Basal Metabolic Rate of a Long-Distance Migrant Shorebird (Red Knot, *Calidris canutus*) Reflects Shifts in Organ Sizes

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Abstract

We studied differences in body composition and basal metabolic rate (BMR, measured in postabsorptive birds under thermoneutral conditions at night) in two subspecies of red knots, Calidris canutus: *one that spends the nonbreeding season under energetically costly climatic conditions at temperate latitudes (subspecies* islandica *in western Europe) and one that winters in the hot and humid tropics (subspecies* canutus *in West and South Africa). To examine whether the possible differences would be upheld under identical conditions, we kept both groups in captivity as well. Body composition was quantified with respect to the fat and lean components of 10 "organs" (breast muscles, leg muscles, stomach, intestine, liver, kidneys, lungs, heart, and the skin, and skeleton and attached muscle). Captive birds had lighter lean tissues than wild birds, especially those of the stomach, intestine, kidneys, and liver (the nutritional organs). During the northern winter wild* islandica *knots had higher lean masses than* canutus *knots in tropical Africa. Tropically wintering red knots had lower BMRs than their temperate-wintering conspecifics, and birds in long-term captivity had lower BMR values than their free-living counterparts. Average BMR values per category of birds (wild or captive of either subspecies) were strongly correlated with the group averages of lean mass. Prediction of BMR on the basis of total lean mass of red knots undergoing incipient starvation follows this same relationship because metabolically active tissue is being depleted. That the two subspecies converged to similar body*

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composition in captivity indicates that individual red knots may possess considerable flexibility. We argue that red knots, and probably most other long-distance migrants, have metabolic machinery that is able to adjust continuously, depending on the ecological conditions and food types encountered in the course of the year. We further argue that variation in (functional components of) lean mass is the vehicle for seasonal adjustments in metabolic physiology to variable demand levels. Body mass adjustments offer a flexible response enabling red knots to economize on total daily metabolic expenditure whenever conditions allow a relaxation of metabolic scope, such as during winter in the Tropics.

Introduction

Birds have a great capacity to track fluctuating resources on a year-round basis by carrying out long-distance migrations (Alerstam 1990). By moving to congenial southern climates during the northern winter, some migrants may reduce the range of climatic conditions they are exposed to (Twomey 1936; Wallgren 1954). Long-distance migrant shorebirds breeding in the high Arctic and wintering at tropical latitudes may increase the variety of encountered climates compared with temperate-resident birds (Drent and Piersma 1990; Piersma, Drent, and Wiersma 1991; Castro, Myers, and Ricklefs 1992; Wiersma and Piersma 1994).

A nice contrast in this respect is provided by two subspecies of red knots, *Calidris canutus* (fig. 1*A*). *Calidris canutus islandica* breeds in high arctic Canada and winters in the cold-temperate climate of western Europe. It does not show great seasonal variability in climate-mediated field metabolic rates (Wiersma and Piersma 1994). *Calidris canutus canutus* breeds in high arctic Siberia, migrates through western Europe, and winters in (sub-)tropical regions in West and South Africa. *Canutus* knots experience great seasonal changes in climate and work level. Red knots always occur in open coastal habitats, fully exposed to climatic conditions. Distribution of red knots could in principle be constrained by ecophysiological limits such as a maximum sustainable metabolic rate (in harsh climates) or a maximum affordable evaporative water loss to cope with the heat load in hot environments (Bartholomew 1958; Prosser 1986; Root 1988; Verboven and Piersma 1995). Thus, we expect that red knots exposed to such different environmental conditions show ecophysiological adjustments (Bartholomew 1958), some of which may be indicated by the differences in their body mass cycles over winter (fig. 1*B* and *C;* and see below). A further question is the extent to which such ecophysiological adjustments are fixed attributes of each subspecies or a general flexible response to environmental conditions.

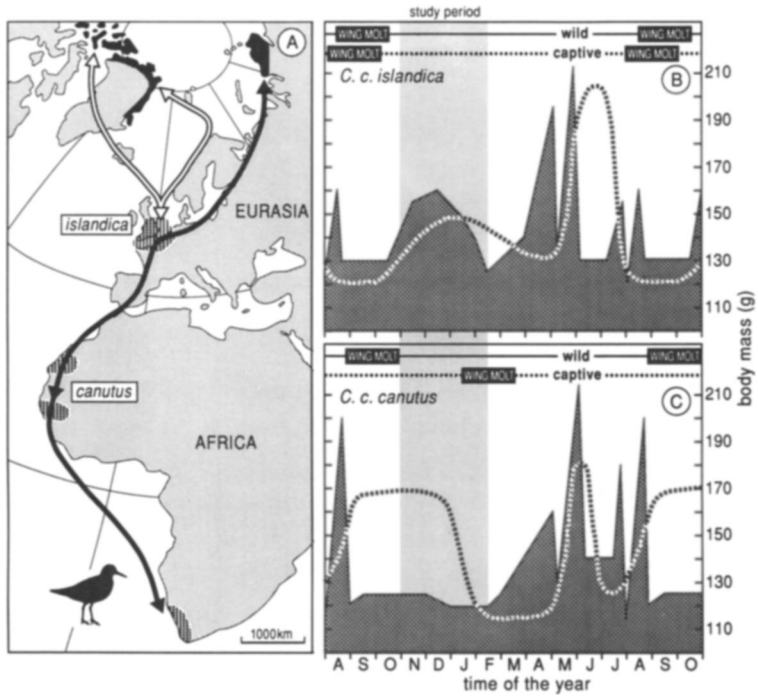

Fig. 1. A, *Migration routes (lines), breeding areas (black), and wintering areas (shaded) of two subspecies of red knots:* Calidris canutus canutus *(linking central Siberia with West Africa; Piersma, Prokosch, and Bredin* [*1992*]*) and* Calidris canutus islandica *(linking the Canadian Arctic and Greenland with western Europe; Davidson and Wilson* [*1992*]*).* B, *Annual cycles in body mass of wild (shaded) and long-term captive (dotted line)* islandica *knots and the timing of their wing molt.* C, *Annual cycles in body mass of wild (shaded) and long-term captive (dotted line)* canutus *knots and the timing of their wing molt. Data for wild birds are from Piersma and Davidson (1992), and for captive birds from T. Piersma (unpublished data). Heavily shaded areas indicate mass changes of free-living birds, and dotted lines indicate average mass changes of captives held in The Netherlands. The timing of wing molt in all groups is indicated by the boxes. In* B *and* C, *the period of the year that this study refers to is indicated by light shading.*

Scholander et al. (1950*a*, 1950*b*, 1950*c*) established a tradition of comparative studies on ecophysiological characteristics of bird and mammal species in relation to energetic demands set by their environments (e.g., Salt 1952; Wallgren 1954; Steen 1958; Dol'nik 1967; Kendeigh and Blem 1974; Weathers 1979; Hails 1983; Hayworth and Weathers 1984; Withers

and Williams 1990). The most commonly used standard for interspecific comparisons in ecological physiology is the basal metabolic rate (BMR) (Bartholomew 1977; Bryant and Tatner 1991). The BMR is the metabolism under the simplest and physiologically least demanding conditions and is operationalized as the metabolic rate of postabsorptive birds resting or sleeping in thermoneutrality in a dark chamber during the rest phase of their daily cycle (Aschoff and Pohl 1970). The practicalities of measuring BMR are straightforward (see Gessaman [1987] for an overview), and although the interpretation of the readings is not without potential methodological biases (see, e.g., Hayes, Speakman, and Racey 1992), BMR has proved reproducible among studies of the same species in different laboratories (e.g., Kersten and Piersma [1987], their table 6).

Although it is thus standard practice to specify the conditions conducive to obtaining strictly comparable determinations of BMR, a complication concerns the variation caused by changes in body mass and composition (see, e.g., Lindström and Piersma 1993). In particular, it would be of obvious value to obtain data on body composition of the experimental subjects. Long ago, Miller and Blyth (1953) advocated reporting BMR in terms of lean body mass to minimize the problem of varying body composition in drawing comparisons. Ideally, metabolic rates should be correlated with the masses of metabolically active tissues.

A classic compilation (Dill, Adolph, and Wilber 1964) and more recent studies (Davidson and Evans 1988; Piersma 1988; Daan et al. 1989; Gaunt et al. 1990; Evans et al. 1992; Piersma, Koolhaas, and Dekinga 1993) show that there is considerable flexibility in organ (including muscle) sizes of individual birds and mammals and that changes are usually directly correlated with field performance or with specific experimental treatments (see, e.g., Brugger 1991; Dykstra and Karasov 1992; Hammond and Diamond 1992). If both BMR and sustained work performance are functions of the supporting metabolic machinery (as suggested by ecologically oriented workers such as Drent and Daan [1980]; Kersten and Piersma [1987]; Daan, Masman, and Groenewold [1990]; Peterson, Nagy, and Diamond [1990]; Daan et al. [1991]; Diamond [1991]), physiological adaptations to environmental conditions (and to peak performance) might be inferred from paired measurements of BMR and body composition in relation to the putative field demands.

This contribution provides such a study. We present an intraspecific comparison of BMR and body composition in four categories of red knots during midwinter, trying to correlate BMR and body composition with each other and with the birds' requirements. We have examined wild birds of the two subspecies described above as well as long-term captive individuals that

faced quite different energetic demands compared with their wild counterparts. Up to now, the literature offers contradictory statements about the effect of captivity on BMR in birds, without consideration of the changes in body composition underlying this. One study on a raptor reports an increase (Warkentin and West 1990), whereas three others on passerine birds detect no changes (Kendeigh 1944; Wallgren 1954; Weathers, Weathers, and van Riper 1983).

Although the two subspecies have only diverged in the recent past, probably less than 10,000 years ago (Baker, Piersma, and Rosenmeier 1994), they show distinct annual cycles (fig. 1*B* and *C*). Temperate-wintering *islandica* knots show a large increase in mass during winter. This peak is completely absent in tropically wintering *canutus* knots. Subspecific differences are even more pronounced in captivity. In captive *islandica* knots the timing of wing molt and the seasonal changes in body mass closely parallel those of birds in the wild (albeit that the multiple body mass peaks during northward and southward migration are replaced by one). The captive *canutus* knots also showed a summer peak in mass but then diverged from the pattern of their wild counterparts by having an extended period of high body mass before loosing mass and starting wing molt in early spring instead of late autumn. This elevated body mass of captive *canutus* knots before wing molt may represent either the physiological preparations for a southward migration or a response to the unexpected photoperiod and/or air temperature prevalent in the outdoor cages in The Netherlands.

Material and Methods

Field Study, Capture, and Collection Sites

Intact carcasses were accumulated from 1979 to 1993. Analyses of body composition (varying in detail) were made on 57 nonbreeding red knots from the German (victims of collision against the Westerhever lighthouse, 54°25′ N, 08°48′ E) and the Dutch Wadden Sea (accidental capture deaths and victims of a natural drowning disaster in thick fog on February 28, 1984), 12 birds from the Arquipélago dos Bijagós in Guinea-Bissau, West Africa (11°30′ N, 15°55′ W), four birds from Langebaan Lagoon in South Africa (33°05′ S, 18°02′ E; all 16 African birds were accidental deaths during and after catching with mist nets in February 1993), and five birds from Iceland (65°35′ N, 23°10′ W; catching casualties from late May, just before their departure to the breeding grounds). We also analyzed 36 red knots that were killed after having been in captivity for at least 1 yr. Finally, a series of starved red knots was examined. Some of them died of starvation in

freezing winter weather in The Netherlands (12 birds), others died on the African study sites (three birds).

Metabolic measurements were made on a more restricted sample of freshly captured red knots from the Wadden Sea in The Netherlands (53°29′ N, 06°12′ E; in November 1988, 1989, and 1991), the Arquipélago dos Bijagós in Guinea-Bissau, West Africa (in February 1993), and Langebaan Lagoon in South Africa (in February and early March 1993). All these birds were captured with mist nets. Additional red knots were caught with mist and cannon nets in the Wadden Sea in The Netherlands and in Germany (54°30′ N, 08°50′ E; in May 1988) and on the Vendée coast of west-central France (45°53′ N, 01°08′ W; in May 1990), to be kept in long-term captivity before being taken into the laboratory for metabolic measurements. All reported metabolic rates were of birds measured in November through early March, that is, outside the migration periods represented by some of the compositionally analyzed birds.

The two subspecies of red knots show only slight differences in morphology (Tomkovich 1992), despite the readily apparent differences in migration pathways and annual mass and molt cycles (fig. 1*A–C*). Red knots from Guinea-Bissau and South Africa were considered to belong to *Calidris canutus canutus,* which breeds in western Siberia (Dick et al. 1976; Piersma et al. 1992). Birds from the Wadden Sea area found dead or captured in the nonbreeding period (October through early April) were all regarded as *Calidris canutus islandica* (Davidson and Wilson 1992). Those that were captured in the second half of May in both west-central France and the German Wadden Sea were considered Siberian-breeding *canutus* (Dick, Piersma, and Prokosch 1987; Piersma et al. 1992). By then all adult *islandica* knots should have left these areas for Iceland or north Norway on their way to the Nearctic tundra (Davidson and Wilson 1992).

Captive red knots were maintained in flocks of 3–10 birds in outdoor cages at the Zoological Laboratory in Haren, The Netherlands (53°11′ N, 06°36′ E). The aviaries had a surface area of 2 × 4 m with a height of 1.8 m. This volume allowed the birds to make short flights. Aviaries contained a freshwater basin with continuously running water. The upper layer of the sandy floor was refreshed every week. The birds were fed with protein-rich pellets of trout food (Trouvit, Produits Trouw, Vervins, France) consisting of 11% water, 12% fiber, 3% cellulose, 45% protein, and 8% fat according to the manufacturer.

With two subspecies (*islandica* and *canutus*) and two ecological treatments (wild and long-term captivity), we had four categories of nonbreeding red knots for analysis. The sex ratio was equal in the sample of 122 red knots for which the most detailed body composition analyses are presented

(overall: 61 males, 57 females, and four unknown; for wild *islandica:* 33 males, 34 females, and two unknown; for wild *canutus:* 11 males and six females; for captive *islandica:* 11 males, 13 females, and one unknown; for captive *canutus:* six males, four females, and one unknown). Van der Meer and Piersma (1994) were unable to show differences between the lean:fat ratio of males and females. The differences in body composition between the *canutus* knots from Guinea-Bissau and South Africa were minimal and are not specifically addressed here.

Analysis of Body Composition

After a couple of months (and up to 4 yr) of storage in airtight plastic bags in deep freezers at −30° to −20°C, carcasses were weighed and dissected. Birds in Guinea-Bissau were not frozen but were dissected within 12 h after death. We measured four external dimensions: wing length (maximum length, with a stopped ruler to the nearest millimeter), bill length (exposed culmen, with calipers to the nearest 0.1 mm), total head length (with calipers to the nearest millimeter), and tarsus plus toe length (with a stopped ruler, excluding the nail of the middle toe, to the nearest millimeter). In addition, we took six internal skeletal dimensions, all connected to the sternum (*a* through *f,* measured with calipers to the nearest 0.01 mm; see Piersma, Davidson, and Evans [1984]; and Jukema and Piersma [1992] for definitions). Sex was determined by gonadal inspection. After plucking the birds, the skin was opened and removed (with the tibiotarsus and feet), and the breast muscles (musculus supracoracoideus and musculus pectoralis) of both sides of the keel were removed. Thereafter, the remaining parts of the body (leg muscle, stomach, intestine, heart, lungs, liver, kidneys, skin, and the rest [including skeleton and attached muscle]) were excised, weighed freshly, and dried separately to constant mass at 55°–60°C.

The dried tissues were packed in filter paper, and the fat was extracted in a Soxhlet apparatus, with petroleum ether (boiling traject 40°–60°C) as the solvent. When the solvent in the extraction vessel no longer showed a yellowish color (indicating fat in solution) for three successive fillings (usually after 4–6 h), fat extraction was considered complete. The body parts were dried to constant mass again and separated from the filter paper, and the remaining lean (fat-free) dry mass was weighed. Fat mass was estimated from the mass loss during extraction.

In this contribution we follow the terminology of Van der Meer and Piersma (1994; their fig. 1). We distinguish between three chemical components (fat, lean dry tissue, and connected water) but basically use a two-component model: lean and fat. Total body mass is the mass of the intact

bird. Lean mass is the body mass minus the mass of extracted fat. Water is a notoriously difficult component to estimate accurately since animals quickly dehydrate both alive and dead (see, e.g., Piersma and Van Brederode 1990). Therefore, we corrected all total body and lean mass values reported here to the overall average water fraction of lean mass (0.6747), assuming that none of the 113 carcasses in a carefully stored subsample of red knots (doubly packed in plastic bags at temperatures below −20°C within 1 d after death) were showing dehydration.

To examine the correlation structure between the size of all parts of the body, a principal components analysis was performed on the correlation matrix of the logarithm of the body parts. Logarithms were taken to approach multivariate normality. The assumption of normality was tested in plots of residuals and found to be reasonable. Each specimen can be conceived as a point in a k-dimensional space, where k is the number of body parts taken into account. The first principal component is a one-dimensional line through the origin on which each data point can be projected. The origin, the center of the graph, represents the average position of all data points. The line is chosen in such a way that the variance of the perpendicular (orthogonal) projections is as large as possible. In a similar way, the first two components span the plane with the highest variance. The position of each projected point on this plane can easily be visualized with reference to figure 2*A*. This figure shows the results of the principal components analysis in the form of a "biplot" (Gabriel 1971). Scales at the axes refer to the principal component scores. The circular perimeter represents the unit scale and indicates the length of the vectors (between 0 and 1, see next paragraph).

Apart from plotting for each specimen the value of the second principal component against the value of the first component, the figure also shows, by means of a vector, the correlation (in the context of principal components analyses often called loading) between each body part and the first two components. The orthogonal projection of each observation on such a vector approximates the value of the accompanying body tissue. The length of the vector indicates the reliability of the approximation. If the vector approaches the full radius, then the approximation is perfect. Note that since the principal components are uncorrelated, the length of the vector is equivalent to R^2, that is, the fraction of the variance of the body parts explained by the first two principal components. The fraction of the total variance that is accounted for by the first two components was equal to 0.70 for the analysis in which all fat and lean parts of tissues were considered ($k = 18$; see fig. 2*A*).

In addition, the correlation between two body parts is indicated by the product of the cosine of the angle between both vectors and the length of the two vectors. Thus, vectors that are pointing in almost the same direction

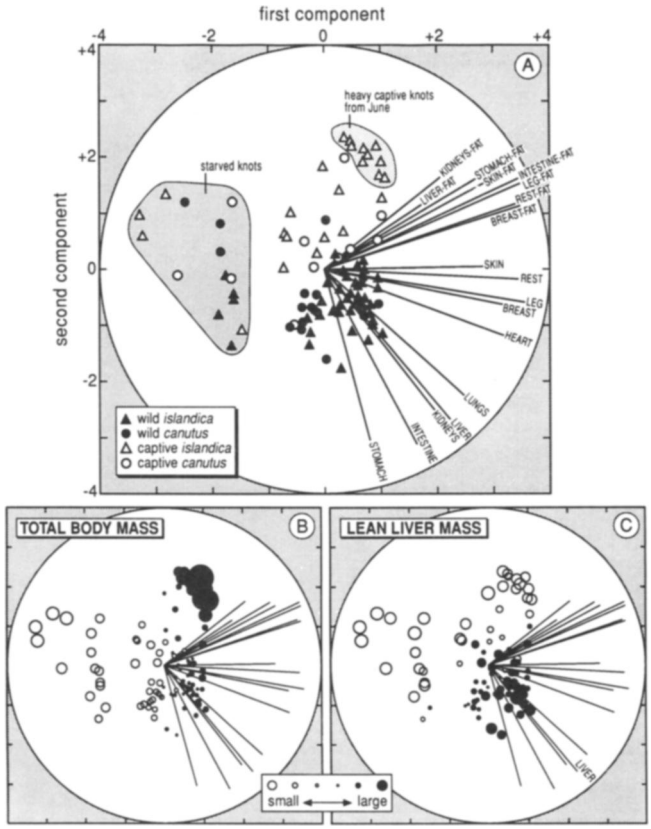

Fig. 2. A, *Biplot of the first two principal components of the logarithms of the lean and fat components of all the parts of the body distinguished in this study. The fat content of all body parts is indicated, as are the lean dry masses of these parts. Lean dry mass of leg muscle is indicated by the term "leg," and the breast muscles by "breast." The first principal component explained 50% of the variance in the data, the second 20% (total* $R^2 = 0.70$*). The two groups of individuals encircled correspond to those in fig. 3*A. B, *The same biplot as* A, *but the diameter and filling of the circles indicate total body mass and illustrate that the first principal component (X-axis) is strongly correlated with it.* C, *The same biplot as* A, *but the diameter and filling of the circles indicate individual red knots with small and large livers.*

and that are both long indicate a highly positive correlation between the body parts involved. A negative correlation is indicated by vectors pointing in opposite directions. Orthogonal vectors indicate zero correlation. Therefore, figure 2*A* shows indications of a correlation between the lean dry masses of kidney and liver. Furthermore, it can be seen that all captive birds show

low values for these body parts. We carried out all these statistical analyses with SYSTAT (Wilkinson 1990).

Respirometry

Red knots from the Wadden Sea were measured within 1 mo after having been transported from the site of capture on the island of Schiermonnikoog to the Zoological Laboratory in Haren. They adjusted readily to their captive condition, did not show any obvious signs of stress, and were fed with pellets of trout food. Freshwater was always available. In Guinea-Bissau and South Africa, metabolic rates of shorebirds were usually measured within a few days after catching them, after which the birds were released. A few red knots were retained in captivity at the study sites for a couple of weeks and measured for a second or third time. Thereafter, they were released as well.

Basal metabolic rates were estimated on the basis of oxygen consumption measurements of postabsorptive birds. All birds, even the seemingly emaciated ones with low fat reserves, had been eating in the days before the experiment. Food, but not water, was taken away for one-half to 1 d before birds were put in the metabolic chamber. The birds were weighed before and after each experiment, but only the initial body masses were used here. For logistic reasons we had to use slightly different systems to measure oxygen consumption at the different study sites, but back home they gave consistent results. In Guinea-Bissau the whole system was set up in the open, but the nights were warm, and box temperatures (20°–27°C) were within the thermoneutral zone of red knots. In South Africa the system was installed in a heated room at 22°–28°C, and in The Netherlands we worked in temperature-controlled cabinets (temperature range 25°–30°C).

Birds were always measured for an entire night at a constant (South Africa and The Netherlands) or near-constant (Guinea-Bissau) air temperature within the thermoneutral zone. Air temperature was registered continuously on a data logger. The metabolic chamber was a dark box of polyvinyl chloride with an air volume of 6–12 L. At all study sites pumps were placed behind the metabolic chamber, and air was thus pumped out. The airflow through the system was set to 40–60 L/h so that oxygen consumption did not exceed 0.5% of the incoming oxygen volume. The measurements in The Netherlands and South Africa were performed with AMETEK applied electrochemistry analyzers (models S-3A and S-3A/II) with an accuracy of 0.002% (manufacturer's calibration). In Guinea-Bissau we used a Servomex 1100A paramagnetic oxygen analyzer with an accuracy of 0.01%. The airflow through respiratory boxes was measured on dry air after passing the animal. Outflowing

air was dried with a molecular sieve (8 Å, Merck; in The Netherlands and South Africa) or silicagel (in Guinea-Bissau). In The Netherlands and South Africa, flow rate was controlled and measured with a Brooks Instruments mass-flow controller (model 5850E) to an accuracy of 1% (manufacturer's calibration), in Guinea-Bissau with a Brooks Sho-rate gravimetric flowmeter. Oxygen consumption was calculated with the appropriate formulas given by Hill (1972) and Withers (1977). The respiratory quotient, RQ, was set to 0.73 (T. Piersma, L. Bruinzeel, and P. Wiersma, personal observation). The metabolic rate, MR, was estimated by assuming an energy equivalent of 20 kJ/L O_2 (Brody 1945, p. 310; Gessaman 1987).

Results

Sex, Subspecies, and Body Size

In the sample of red knots of which body composition was examined, there were significant differences between the sexes and subspecies in the length of the following external dimensions: wing ($F_{2,85} = 7.1$, $P = 0.001$), bill ($F_{2,85} = 11.8$, $P < 0.001$), and total head ($F_{2,85} = 9.4$, $P < 0.001$). Also, in the internal dimensions—the height of the keel of the sternum, b ($F_{2,85} = 4.8$, $P = 0.010$), and the width of the sternum, d ($F_{2,85} = 7.4$, $P = 0.001$)—there were significant differences between sexes and subspecies; the dimensions of males were always smaller than those of females (average 0.57 mm for bill length), and those of *Calidris canutus islandica* were smaller than those of *Calidris canutus canutus* (average 0.90 mm for bill length). This analysis was based on the fact that there were no significant interactions between sex and subspecies with respect to external or internal dimensions. Our results are in accordance with findings reported in the literature (Dick et al. 1976; Roselaar 1983; Tomkovich 1992), although the absolute differences in bill and wing lengths are somewhat smaller.

Body Composition

A reasonable first question is whether captive birds maintain the same lean: fat composition as their wild conspecifics. A plot of lean mass (calculated from lean dry mass and an average water content of 67.47%) on fat mass (fig. 3*A*) shows (1) that there is a breakpoint in body composition at a fat mass of about 5 g and a lean mass of 100–110 g, (2) that wild birds of both subspecies seem to have higher lean masses at the same fat mass above the breakpoint than do captive birds, and (3) that there is only a small increase in lean mass at increasing fat mass above the breakpoint in both the wild

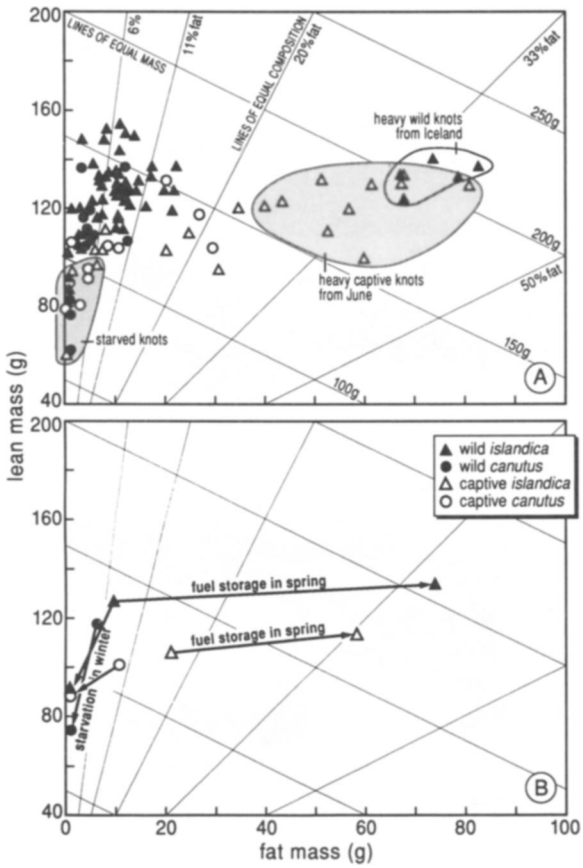

Fig. 3. Two-component interpretation of variations in body composition of red knots of four categories. A, *Plot of total lean mass on fat mass also showing lines of equal mass and of equal composition (see Van der Meer and Piersma 1994). Three groups of individuals are circled to enable a comparison with fig. 2*A. B, *The averages for the heavy captive* islandica *knots from June and the birds from Iceland along with the lean:fat ratio of birds of three categories in the winter season (November through early March) and after having starved to death. This illustrates the body composition trajectories that individual birds may go through during fuel deposition before northward migration and during starvation in winter. The Icelandic birds were not analyzed in great detail and do not appear elsewhere in the article.*

and captive groups of *islandica* knots, a conclusion reached earlier by Van der Meer and Piersma (1994) for a different sample of red knots. Figure 3*B* shows how individual birds (on the basis of averages for groups) may change in the lean:fat proportions from a midwinter condition (the three symbols

in the middle) to a migratory-departure condition as illustrated by the average for five birds from Iceland in late May (toward the right) or toward dead by starvation (toward the left). During starvation the wild birds mainly use up lean tissue.

A biplot of the lean and fat mass of different body parts (fig. 2*A*) shows (1) that the fat contents of different body parts are strongly correlated with each other, more so than the lean body parts, (2) that fat and lean contents of body parts are poorly correlated with each other or not at all, and (3) that, except for a group of starved birds, the captive red knots show a distinctly different distribution in the principal component plane than the wild birds. Although the long-term captive birds showed slightly more liver and kidney fat and project similarly on the other fat vectors, they show smaller lean tissues, especially the stomach, intestine, kidneys, and liver. The fat contents of most parts of the body are strongly intercorrelated, except for the fat contents of kidneys and liver, for which the short vectors indicate that they are poorly correlated with other fat deposits (fig. 2*A*).

In figure 3*A* we highlight three groups of individual birds, two of which are familiar from figure 2*A,* to allow a recognition of the similarities and differences in information content of the two types of graph. The group of starved birds with very low body masses is easy to recognize in both kinds of plots: the first principal component in figure 2*A* clearly indicates total body mass, and this is made explicit in figure 2*B*. Starved knots show particularly low projections on the fat axes and on the axes of skin, skeleton and attached muscle (the rest), leg muscle, breast muscle, and heart. The heavy *islandica* captives can be recognized since they project highly on the fat axis in figure 3*A* and the fat vectors in figure 2*A*. By way of example, figure 2*C* illustrates how birds with variably sized livers project on the axis for lean liver mass.

There are two groups of vectors for lean body parts, groups of tissues that poorly intercorrelate (fig. 2*A*). The first group includes the skin, the skeleton and attached muscle (the rest), the leg muscles, the breast muscles, and the heart (the muscles group, since even the "rest" category contains many groups of small muscles connected to the skeleton). The second group includes the liver, the kidneys, the intestine, and the stomach. These four organs will be called the nutritional organs. The lungs are intermediate between the two groups of body parts. Although the first principal component in the biplots clearly represented total lean dry mass of the birds ($r = 0.96$), it was not correlated with the four external and six internal dimensions. The lean dry mass of the muscles group correlated best with the first principal component and with total lean dry mass, whereas the nutritional organs show another pattern. Small nutritional organs are found in

the northwestern half of the biplot, thus comprising the category of captive red knots of both subspecies (fig. 2*A*).

In order to correct for the variations in absolute size, we made a biplot of the relative contributions of lean dry masses of body parts scaled to lung mass (fig. 4*A*). The resulting principal components do not depend on the choice of the common denominator (Aitchison 1986). The two groups of body parts are even more obvious in this analysis than in figure 2, as indicated by the two tight bunches of vectors. The relative sizes of muscles and nutritional organs are not correlated at all. Nutritional organs are relatively small in captive birds, but muscles are not.

To summarize and evaluate the differences between the four categories of red knots, figure 4*B* presents the dimensionless ratios of the lean dry mass of the nutritional organ group divided by the lean dry mass of muscles. Captive and wild birds are well separated by this ratio. Figure 4*B* suggests that *islandica* knots may respond more strongly to captive conditions in the temperate zone (by decreasing lean mass and the size of their nutritional organs) than *canutus* knots. This striking discrepancy may be an effect of *canutus* knots' being relatively heavy in captivity during the northern winter compared with their wild counterparts in tropical Africa (see fig. 1*C*).

Table 1 summarizes the differences in lean dry mass and body composition of the four categories of red knots. These are slightly more restricted groupings (collected from November to February, nonemaciated birds only), and for these we will present metabolic data. Intestine, stomach, skeleton and attached muscle (the rest), heart, and skin showed the highest values in wild, temperate-wintering *islandica* knots (table 1). The nutritional organs accounted for most (51%–65%) of the decreased lean dry mass of captive red knots compared with that of wild birds.

Mass-Dependent Variation in BMR

The BMR differed among the four categories of birds (ANOVA, $R^2 = 0.51$, $F_{3,37} = 12.7$, $P < 0.0001$; fig. 5*A*). The BMR was significantly higher in wild *islandica* knots than in wild *canutus* knots, while BMR of captive birds was significantly reduced compared with that of wild birds (Scheffé tests). However, BMR did not differ between the two subspecies when kept in captivity.

The relationship between BMR and total body mass is weak at best (fig. 5*C*), and nearly all variation in the average BMR per category was explained by corresponding variation in lean mass (fig. 5*B*). This suggests that lean

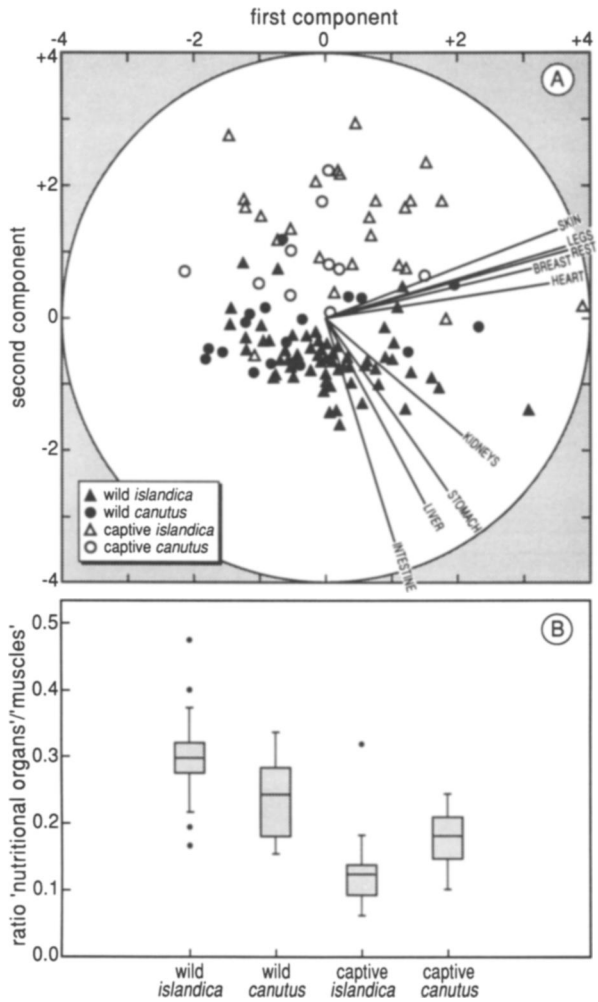

Fig. 4. A, *Relative contributions to lean dry mass of different parts of the body represented by a biplot of the first two principal components of the logarithms of the ratios of lean dry mass of a body part and lean dry mass of the lungs of four categories of red knots. The first principal component explained 50% of the variance in the data, the second, 24% (total* $R^2 = 0.73$*). Since lean dry mass of lungs was used to scale the other body parts, the vector for lungs is absent.* B, *Box plot of the dimensionless ratios of the masses of the nutritional organ and muscle groups identified in* A *(i.e., the summed mass of intestine, liver, stomach, and kidneys divided by the summed mass of heart, breast muscle, skeleton and attached muscle [the rest], leg muscle, and skin) of four categories of red knots. The box plot gives median ± 25% quartiles as a box and indicates range (vertical lines) and outliers (small dots).*

TABLE 1

Differences in the composition of the lean body mass (g) of wild and captive Calidris canutus islandica *and* Calidris canutus canutus *for the midwinter period*

Body Part	Wild Birds		Captive Birds	
	Calidris canutus islandica (n = 33)	*Calidris canutus canutus* (n = 13)	*Calidris canutus islandica* (n = 4)	*Calidris canutus canutus* (n = 3)
Total body mass	142.6 ± 13.7	124.5 ± 12.4	134.9 ± 15.3	124.3 ± 14.2
Lean mass	131.1 ± 12.0	117.7 ± 10.7	104.0 ± 6.9	108.8 ± 6.1
Lean dry mass	42.69 ± 3.88	38.29 ± 3.48	33.85 ± 2.24	35.29 ± 1.99
Dry feather mass	8.13 ± .87	6.75 ± .34	6.65 ± .69	5.79 ± .38
Stomach	3.06 ± .45	2.57 ± .55	.81 ± .06	1.03 ± .17
Intestine	2.44 ± .45	1.77 ± .55	.70 ± .23	1.33 ± .42
Kidneys	.47 ± .14	.48 ± .11	.40 ± .03	.46 ± .12
Liver	1.64 ± .26	1.55 ± .28	1.18 ± .44	1.60 ± .30
Nutritional organs	7.61	6.37	3.09	4.42
Lungs	.57 ± .39	.59 ± .14	.45 ± .18	.65 ± .12
Heart	.54 ± .08	.46 ± .12	.46 ± .08	.46 ± .10
Breast muscles	7.30 ± 1.26	7.23 ± 1.14	6.48 ± .29	5.49 ± .71
Leg muscles	1.01 ± .15	.93 ± .14	.94 ± .11	1.09 ± .15
Rest	12.86 ± 1.30	11.61 ± 1.04	11.76 ± .84	13.29 ± .81
Skin	4.64 ± 1.37	3.90 ± 1.02	4.00 ± .53	4.19 ± .24
Muscles	26.35	24.13	23.64	24.52

Note. Values presented are mean ± SD.

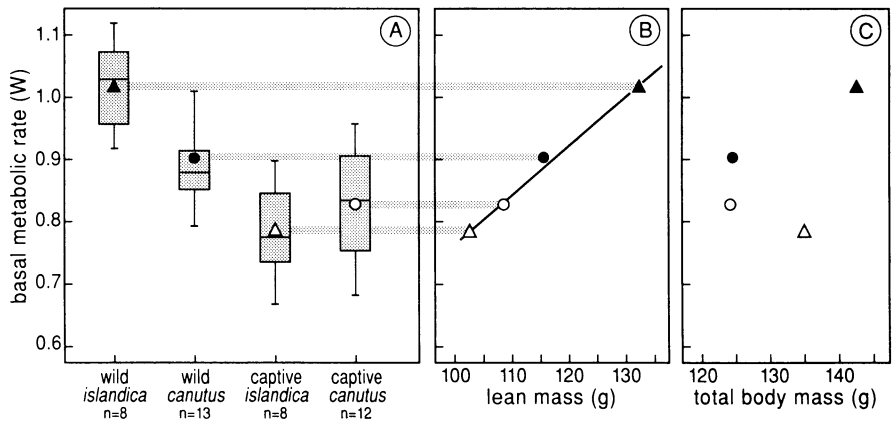

Fig. 5. A, *Box plot of BMR of wild and long-term captive* Calidris canutus islandica *and* Calidris canutus canutus *knots (nonemaciated birds that are predicted to contain more than 3 g fat).* B, *The BMR as a function of category-specific averages of lean mass (LM; table 1). The regression line is fitted through the four averages and given by the equation BMR* $= 0.0088 \cdot LM - 0.129$ *(*n $= 4$, $R^2 = 1.00$*).* C, *The BMR as a function of category-specific averages of total body mass (TBM; table 1). The regression line (not depicted) is given by the equation BMR* $= 0.0058 \cdot TBM + 0.124$ *(*n $= 4$, $R^2 = 0.24$*). Category-specific averages of lean mass are used because birds were not sacrificed and compositionally analyzed after BMR measurements.*

mass alone determines BMR, but this interpretation is probably not correct. The BMR differed considerably between individuals, but these measurements were lumped for each category since we do not know the actual lean mass of each individual bird.

How does this relationship change when body mass (and therefore lean mass, mainly in the muscles group) declines during starvation? As it happens, we do have data on this topic on account of the refusal of some individuals captured in Guinea-Bissau and South Africa to fully adapt to our holding conditions and food regime. Body mass in some red knots fell below 110 g, below which point they carried an average of 1.1 g fat (as illustrated in fig. 3*A*). In figure 6 we have plotted measured BMR during incipient starvation as a function of predicted lean mass of *canutus* knots. The BMR of these nutritionally depleted birds is close to what we would predict on the basis of extrapolations of values for birds in figure 5*B*, even though the losses in lean mass refer to muscle tissue rather than to the nutritional organs (fig. 2*A*).

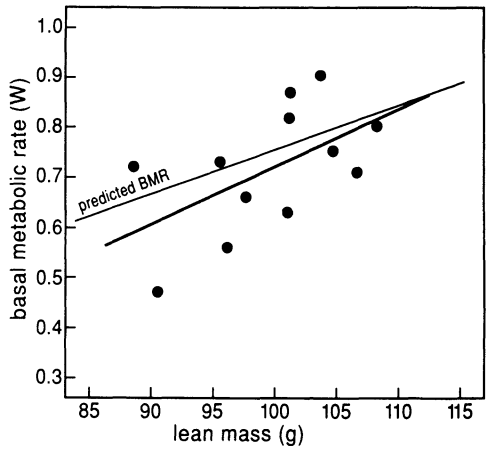

Fig. 6. Basal metabolic rate of wild Calidris canutus canutus *knots in the body mass trajectory where almost all mass changes are in lean tissue, as a function of their estimated lean mass (i.e., body mass minus the average 1.1 g of fat found in such birds). The predicted BMR value (on the basis of the equation from fig. 5B) is given with the linear regression line for the data points for wild* canutus *knots (equation BMR = 0.0115 · LM − 0.429,* n = *12,* R^2 = *0.31).*

Discussion

Physiological Adjustments to Cage Conditions

Earlier, a severe reduction in stomach mass was described for red knots that were fed soft food pellets in captivity (Piersma et al. 1993). Red knots that have become accustomed to eating pellets seem reluctant to feed on their normal hard-shelled mollusc prey when offered again. Changes in stomach size as a function of diet type are known for numerous other species as well (review in Piersma et al. [1993]). This list may now be extended to other parts of the nutritional system, especially the intestine (for other examples, see Moss [1972]; Brugger [1991]) and to a lesser extent the liver and the kidney. But why do caged birds show atrophy of their nutritional organs and not of their skeletal musculature?

Locomotory muscles of mammals that are experimentally immobilized show immediate disuse atrophy (Summers and Hines 1951; Ferguson, Vaughan, and Ward 1957; Booth and Gollnick 1983). That there is no atrophy of locomotory muscles in caged birds suggests that, even in cages, breast and leg muscles of red knots get enough exercise to retain their normal size. Given that many muscles are active even when standing in a resting position (Gordon 1977), this may not be surprising. Note that wild red knots

are known to enlarge their breast muscles before takeoff on long-distance flights (Davidson and Evans 1988; Evans et al. 1992), and we have found the same in birds under captive conditions (T. P. Weber and T. Piersma, personal observation).

The reduction in stomach size in captive birds can easily be explained by the fact that the stomach no longer has to do the muscular work to crack ingested molluscs. It shows disuse atrophy (Goldberg 1972; Booth 1977). However, this does not necessarily need to lead to decreased size of the intestine, liver, and kidneys (Brugger 1991). Only by assuming that the lower work levels (thermoregulation and exercise) of birds in cages lead to a lower work pressure on these organs can we invoke disuse atrophy as the explanation. If animals try to minimize maintenance costs, one obvious way would be to adjust the mass of the nutritional organs to required capacity, whatever the mechanism is.

Basal Metabolic Rate Reflects Lean Mass

The BMR varies with lean mass. Our results support the notion that fat is metabolically a relatively inactive tissue (Aschoff, Günther, and Kramer 1971; Blaxter 1989; Scott and Evans 1992). The difficulty of assessing fat or lean mass without sacrificing the animal (see, e.g., Van der Meer and Piersma 1994) must explain the paucity of attempts to express BMR as a function of lean mass rather than total body mass, in spite of the early advocacy of Miller and Blyth (1953).

Is it possible to assign differences in BMR to differences in the size of specific organs (Daan et al. 1990)? Table 1 indicates that most of the differences between the groups are due to size differences in the nutritional organs, notably the stomach and the intestine. These comprise 11% (wild *Calidris cantutus canutus*) to 13% (wild *Calidris cantutus islandica*) of the lean dry mass. Since we have no data on tissue respiration of these organs, detailed evaluation of the relative contribution of the organ mass differences to BMR cannot at present be made. The different gut sizes of the various categories of red knots are likely to be a major factor influencing BMR. In ruminant mammals, the energetic cost of maintaining the gut contributes up to 40% of BMR (Webster 1981). However, during incipient starvation it is a decrease in the size of the skeletal musculature and heart that leads to a further reduction in BMR.

Adaptations in Lean Mass?

Piersma et al. (1991) alluded to the possibility that BMR in different subspecies of red knots is adapted to the climatic conditions of their winter quarters. We

should like to take this one step further and state that lean mass has in fact primacy, with the organs making up lean mass being adjusted to climatic and food conditions and BMR's being adjusted as a consequence. When work levels are low and relatively constant, intake rates can be low, and the body can do with a relatively small support machinery (i.e., the nutritional organs). The combination of low lean mass and BMR in tropically wintering *canutus* knots has the additional benefit of preventing the need for extensive evaporative cooling when external heat loads are high (Klaassen, Kersten, and Ens 1990; Verboven and Piersma 1995). A high lean mass (and, consequently, a high BMR) in temperate-wintering *islandica* knots also makes sense since the high required intake rate and high energy expenditure necessitate a high support capacity (i.e., large nutritional organs). This capacity would also yield additional metabolic scope to overcome periods of severe cold stress in the energetically demanding climate of the northern mudflats (Kersten and Piersma 1987; Wiersma and Piersma 1994) (fig. 7*A*).

The fact that *islandica* and *canutus* knots converged to become rather similar birds under the relaxed environmental conditions in captivity suggests that both subspecies possess the flexibility to reduce the machinery to support elevated working levels and hence save on energy expenditure. In order to convincingly demonstrate that this flexibility is reciprocal, experimental treatments with changed photoperiod (for *islandica* knots), changed energy demand levels (for *canutus* knots), and changed food type (i.e., molluscs, for both subspecies) are called for. Nevertheless, the finding that red knots show breast muscle hypertrophy during migratory fat deposition and show atrophy afterward indicates that additional dimensions of flexibility must exist. The combination of the latter mechanisms and the flexibility documented in this article should allow individual red knots to adjust to the full range of climatic conditions they are exposed to in the course of the year (Piersma et al. 1991; Piersma, Codée, and Daan 1995).

In the study of intraspecific variation in BMR in North American house sparrow (*Passer domesticus*) populations, Hudson and Kimzey (1966) were impressed with the distinction between a Texas population and the more northerly birds. They concluded that metabolism "exhibits adaptive modification to cope with an environment of high temperatures and high humidities" (p. 214). Since these resident populations derive from a unitary introduction (Johnston and Selander 1964), this difference must have arisen through evolutionary change in the past century. Hudson and Kimzey reasoned from the persistence of the metabolic difference throughout protracted periods of captivity when all populations were exposed to the same conditions that the low rate of metabolism of the Texas birds had become genetically fixed. Although they did not examine body composition, their

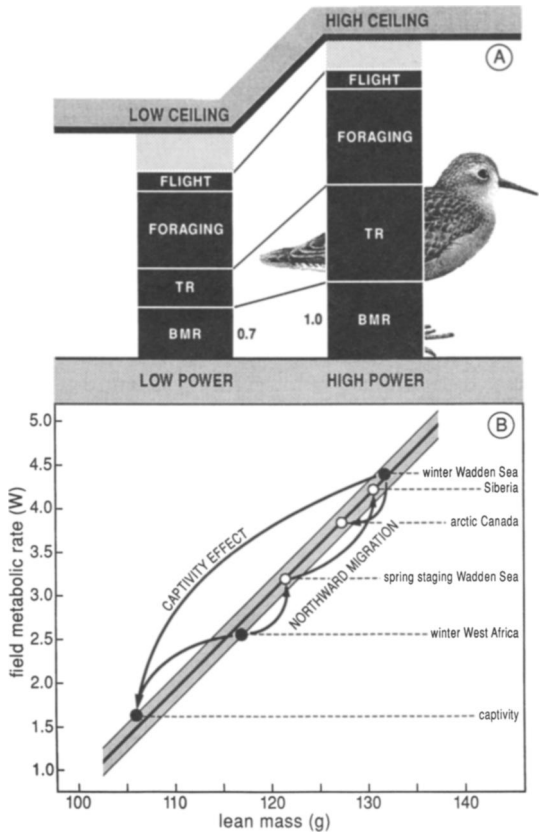

Fig. 7. A, *Illustration of the elevated working capacity of birds with a high lean mass indicative of a large support machinery (high-power mode) relative to that of downsized individuals (low-power mode). Most of the metabolic expansion is devoted to increased thermoregulation (TR) and foraging/locomotory costs.* B, *Correlation between lean mass and field metabolic rates. This study has suggested that low- and high-powered knots are characterized by small and large lean masses, respectively, which in turn are empirically correlated with (and a possible function of) field metabolic rates. Filled dots are the data points reported in this study, with the values for two subspecies in captivity being averaged. The open circles indicate the putative levels in other parts of the year for the two subspecies (plotted on the regression line through the three empirical data points): the spring staging areas in the Wadden Sea and the Siberian breeding grounds for* Calidris canutus canutus *and the Canadian breeding grounds for* Calidris canutus islandica. *Field metabolic rates are estimated from predictions of maintenance metabolism (Wiersma and Piersma 1994), estimated costs of activity in the various conditions (M. Poot and T. Piersma, personal observation), and unpublished doubly labeled water measurements on field metabolic rates in the Siberian Arctic (T. Piersma, personal observation).*

conclusion about BMR seems to contrast with the flexibility of red knots. In our view the migratory habit bringing all knot populations into thermally similar environments at least part of the year has precluded the establishment of subspecific divergence in metabolic intensity on a year-round basis. The impressive differences in wintering conditions experienced by the two subspecies we studied are effectively dealt with by an adaptive syndrome involving a circannual program of change in total body mass and composition (see also Piersma et al. 1995).

Figure 7*B* summarizes our views on seasonal change in work level (in this case, represented by field metabolic rate of the two knot populations studied) and how these changes impinge on lean mass in long-distance migrant shorebirds. (For illustrative reasons, lean mass is placed on the *X*-axis.) Seasonal peaks in metabolic requirements will be financed by adaptive increases in lean mass (note the presumed qualitative reversal of the two populations during breeding), whereas benign wintering conditions (such as those experienced by *canutus* knots in Africa and red knots in captivity) induce a marked reduction in lean mass. This jettisoning of surplus body tissue, in particular the nutritional support systems of the body, lowers BMR and thus the cost of maintenance. A lower level of endogenous heat production may be advantageous under conditions of heat stress, whereas decreased body mass leads to considerable savings in the daily costs of locomotion since these increase with body mass (Taylor, Heglund, and Maloiy 1982). The ecological significance of these daily savings is made clear with reference to the doubly labeled water determinations of foraging red knots on a tidal flat (M. Poot and T. Piersma, unpublished observations), where locomotion costs (walking) loomed large in the daily energy budget (45%). We espouse the view that an increase in lean mass (fig. 7*B*) is an adaptive response enabling an appropriate increase in metabolic scope (fig. 7*A*) without precluding the option of direct energetic savings whenever the enlarged tissues can be dispensed with.

Studies on the size variation of different muscle and organ groups under various demand regimes, coupled with a quantification of the energetic repercussions of such size differences, are likely to generate considerable insight into the adaptiveness of variations in body composition as well as BMR. Long-distance migrant shorebirds provide interesting and workable models for such studies.

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Literature Cited

AITCHISON, J. 1986. The statistical analysis of compositional data. Chapman & Hall, London.

ALERSTAM, T. 1990. Bird migration. Cambridge University Press, Cambridge.

ASCHOFF, J., B. GÜNTHER, and K. KRAMER. 1971. Energieaushalt und Temperaturregulation. Urban & Schwarzenberg, Berlin.

ASCHOFF, J., and H. POHL. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergrösse. J. Ornithol. 111:38–47.

BAKER, A. J., T. PIERSMA, and L. ROSENMEIER. 1994. Unraveling the intraspecific phylogeography of knots *Calidris canutus:* a progress report on the search for genetic markers. J. Ornithol. 135:599–608.

BARTHOLOMEW, G. A. 1958. The role of physiology in the distribution of terrestrial vertebrates. Pp. 81–95 in C. L. HUBBS, ed. Zoogeography. Publication no. 51. American Association for the Advancement of Science, Washington, D.C.

———. 1977. Energy metabolism. Pages 57–110 in M. S. GORDON, ed., Animal physiology: principles and adaptations. Macmillan, New York.

BLAXTER, K. 1989. Energy metabolism in animals and man. Cambridge University Press, Cambridge.

BOOTH, F. W. 1977. Time course of muscular atrophy during immobilization of hindlimbs of rats. J. Appl. Physiol. 43:656–661.

BOOTH, F. W., and P. D. GOLLNICK. 1983. Effects of disuse on the structure and function of skeletal muscle. Med. Sci. Sports Exerc. 15:415–420.

BRODY, S. 1945. Bioenergetics and growth. Reinhold, New York.

BRUGGER, K. E. 1991. Anatomical adaptation of the git to diet in red-winged blackbirds (*Agelaius phoeniceus*). Auk 108:562–567.

BRYANT, D. M., and P. TATNER. 1991. Intraspecies variation in avian energy expenditure: correlates and constraints. Ibis 133:236–245.

CASTRO, G., J. P. MYERS, and R. E. RICKLEFS. 1992. Ecology and energetics of sanderlings migrating to four latitudes. Ecology 73:833–844.

DAAN, S., D. MASMAN, and A. GROENEWOLD. 1990. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. Am. J. Physiol. 259:R333–R340.

DAAN, D., D. MASMAN, A. STRIJKSTRA, and G. J. KENAGY. 1991. Daily energy turnover during reproduction in birds and mammals: its relationship to basal metabolic rate. Pages 1976–1987 in B. D. BELL, R. O. COSSEE, J. E. C. FLUX, B. D. HEATHER, R. A. HITCHMOUGH, C. J. R. ROBERTSON, and M. J. WILLIAMS, eds. Acta XX Congressus Internationalis Ornithologici. Christchurch.

DAAN, S., D. MASMAN, A. STRIJKSTRA, and S. VERHULST. 1989. Intraspecific allometry of basal metabolic rate: relations with body size, temperature, composition, and circadian phase in the kestrel, *Falco tinnunculus.* J. Biol. Rhythms 4:267–283.

DAVIDSON, N. C., and P. R. EVANS. 1988. Prebreeding accumulation of fat and muscle protein by arctic-breeding shorebirds. Pages 342–352 in H. OUELLET, ed. Acta XIX Congressus Internationalis Ornithologici. University of Ottawa Press, Ottawa.

DAVIDSON, N. C., and J. R. WILSON. 1992. The migration system of European-wintering knots *Calidris canutus islandica.* Wader Study Group Bull. 64(suppl.):39–51.

DIAMOND, J. 1991. The athlete's dilemma. Discover (August 1991): 78–83.

DICK, W. J. A., M. W. PIENKOWSKI, M. WALTNER, and C. D. T. MINTON. 1976. Distribution and geographical origins of knot *Calidris canutus* wintering in Europe and Africa. Ardea 64:22–47.

DICK, W. J. A., T. PIERSMA, and P. PROKOSCH. 1987. Spring migration of the Siberian knots *Calidris canutus canutus:* results of a co-operative Wader Study Group project. Ornis Scand. 18:5–16.

DILL, D. B., E. F. ADOLPH, and C. G. WILBER, eds. 1964. Handbook of physiology. Sec. 4. Adaptation to the environment. American Physiological Society, Washington, D.C.

DOL'NIK, V. R. 1967. Bioenergetische Anpassungen der Vögel an die Überwinterung in verschiedenen Breiten. Falke 9:305–306, 347–349.

DRENT, R. H., and S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.

DRENT, R., and T. PIERSMA. 1990. An exploration of the energetics of leap-frog migration in arctic breeding waders. Pages 399–412 in E. GWINNER, ed. Bird migration: physiology and ecophysiology. Springer, Berlin.

DYKSTRA, C. R., and W. H. KARASOV. 1992. Changes in gut structure and function of house wrens (*Troglodytes aedon*) in response to increased energy demands. Physiol. Zool. 65:422–442.

EVANS, P. R., N. C. DAVIDSON, J. D. UTTLEY, and R. D. EVANS. 1992. Premigratory hypertrophy of flight muscles: an ultrastructural study. Ornis Scand. 23:238–243.

FERGUSON, A. B., L. VAUGHAN, and L. WARD. 1957. A study of disuse atrophy of skeletal muscle in the rabbit. J. Bone Joint Surg. 39A:583–596.

GABRIEL, K. R. 1971. The biplot graphic display of matrices with application to principal components analysis. Biometrika 58:453–467.

GAUNT, A. S., R. S. HIKIDA, J. R. JEHL, JR., and L. FENBERT. 1990. Rapid atrophy and hypertrophy of an avian flight muscle. Auk 107:649–659.

GESSAMAN, J. A. 1987. Energetics. Pages 289–320 in B. A. GIRON PENDLETON, B. A. MILLSAP, K. W. CLINE, and D. M. BIRD, eds. Raptor management techniques manual. National Wildlife Federation, Washington, D.C.

GOLDBERG, A. L. 1972. Mechanisms of growth and atrophy of skeletal muscle. Pages 89–118 in R. G. CASSENS, ed. Muscle biology. Dekker, New York.

GORDON, M. S. 1977. Movement: the physiology of muscle. Pages 111–155 in M. S. GORDON, ed. Animal physiology: principles and adaptation. Macmillan, New York.

HAILS, C. J. 1983. The metabolic rate of tropical birds. Condor 85:61–65.

HAMMOND, K. A., and J. DIAMOND. 1992. An experimental test for a ceiling on sustained metabolic rate in lactating mice. Physiol. Zool. 65:952–977.

HAYES, J. P., J. R. SPEAKMAN, and P. A. RACEY. 1992. Sampling bias in respirometry. Physiol. Zool. 65:604–619.

HAYWORTH, A. M., and W. W. WEATHERS. 1984. Temperature regulation and climatic adaptation in black-billed and yellow-billed magpies. Condor 86:19–26.

HILL, R. N. 1972. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. J. Appl. Physiol. 33:261–263.

HUDSON, J. W., and S. L. KIMZEY. 1966. Temperature regulation and metabolic rhythms in populations of the house sparrow *Passer domesticus*. Comp. Biochem. Physiol. 17:203–217.

JOHNSTON, R. F., and R. K. SELANDER. 1964. House sparrows: rapid evolution of races in North America. Science 144:548–550.

JUKEMA, J., and T. PIERSMA. 1992. Golden plovers *Pluvialis apricaria* do not show sexual dimorphy in external and internal linear dimensions (in Dutch with English summary). Limosa 65:147–154.

KENDEIGH, S. C. 1944. Effect of air temperature on the rate of energy metabolism in the English sparrow. J. Exp. Zool. 96:1–16.

KENDEIGH, S. C., and C. R. BLEM. 1974. Metabolic adaptation to local climate in birds. Comp. Biochem. Physiol. 48A:175–187.

KERSTEN, M., and T. PIERSMA. 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. Ardea 75:175–187.

KLAASSEN, M., M. KERSTEN, and B. J. ENS. 1990. Energetic requirements for maintenance and premigratory body mass gain of waders wintering in Africa. Ardea 78:209–220.

LINDSTRÖM, Å., and T. PIERSMA. 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. Ibis 135:70–78.

MILLER, A. T., and C. S. BLYTH. 1953. Lean body mass as a metabolic reference standard. J. Appl. Physiol. 5:311–316.

MOSS, R. 1972. Effects of captivity on gut lengths in red grouse. J. Wildl. Manage. 36:99–104.

PETERSON, C. C., K. A. NAGY, and J. A. DIAMOND. 1990. Sustained metabolic scope. Proc. Natl. Acad. Sci. USA 87:2324–2328.

PIERSMA, T. 1988. Breast muscle atrophy and constraints on foraging during flightless periods of wing moulting great crested grebes. Ardea 76:96–106.

PIERSMA, T., N. CADÉE, and S. DAAN. 1995. Seasonality in basal metabolic rate and conductance in a long-distance migrant shorebird, the knot. J. Comp. Physiol. 165B:37–45.

PIERSMA, T., and N. C. DAVIDSON. 1992. The migrations and annual cycles of five subspecies of knots in perspective. Wader Study Group Bull. 64(suppl.):187–197.

PIERSMA, T., N. C. DAVIDSON, and P. R. EVANS. 1984. Estimation of the protein reserves of waders: the use and misuse of standard muscle volume. Wader Study Group Bull. 42:19–22.

PIERSMA, T., R. DRENT, and P. WIERSMA. 1991. Temperate versus tropical wintering in the world's northernmost breeder, the knot: metabolic scope and resource levels restrict subspecific options. Pages 761–772 in B. D. BELL, R. O. COSSEE, J. E. C. FLUX, B. D. HEATHER, R. A. HITCHMOUGH, C. J. R. ROBERTSON, and M. J. WILLIAMS, eds. Acta XX Congressus Internationalis Ornithologici. Christchurch.

PIERSMA, T., A. KOOLHAAS, and A. DEKINGA. 1993. Interactions between stomach structure and diet choice in shorebirds. Auk 110:552–564.

PIERSMA, T., P. PROKOSCH, and D. BREDIN. 1992. The migration system of Afro-Siberian knots *Calidris canutus canutus*. Wader Study Group Bull. 64(suppl.):52–63.

PIERSMA, T., and N. E. VAN BREDERODE. 1990. The estimation of fat reserves in coastal waders before their departure from northwest Africa in spring. Ardea 78:221–236.

PROSSER, C. L. 1986. The challenge of adaptational physiology. Physiologist 29:2–4.

ROOT, T. 1988. Energy constraints on avian distributions and abundances. Ecology 69:330–339.

ROSELAAR, C. S. 1983. Subspecies recognition in knot *Calidris canutus* and occurrence of races in western Europe. Beaufortia 33:97–109.

SALT, G. W. 1952. The relation of metabolism to climate and distribution in three finches of the genus *Carpodacus*. Ecol. Monogr. 22:121–152.

SCHOLANDER, P. F., R. HOCK, V. WALTERS, and L. IRVING. 1950*a*. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biol. Bull. 99:259–271.

SCHOLANDER, P. F., R. HOCK, V. WALTERS, F. JOHNSON, and L. IRVING. 1950*b*. Heat regulation in some arctic and tropical mammals and birds. Biol. Bull. 99:237–258.

SCHOLANDER, P. F., V. WALTERS, R. HOCK, and L. IRVING. 1950*c*. Body insulation of some arctic and tropical mammals and birds. Biol. Bull. 99:225–236.

SCOTT, I., and P. R. EVANS. 1992. The metabolic output of avian (*Sturnus vulgaris, Calidris alpina*) adipose tissue, liver and skeletal muscle: implications for BMR/body mass relationships. Comp. Biochem. Physiol. 103A:329–332.

STEEN, J. 1958. Climatic adaptations in some small northern birds. Ecology 39:625–629.

SUMMERS, T. B., and H. M. HINES. 1951. Effect of immobilization in various positions upon the weight and strength of skeletal muscle. Arch. Physiol. Med. 32:142–145.

TAYLOR, C. R., N. C. HEGLUND, and G. M. O. MALOIY. 1982. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. J. Exp. Biol. 97:1–21.

TOMKOVICH, P. S. 1992. An analysis of the geographic variability in knots *Calidris canutus* based on museum skins. Wader Study Group Bull. 64(suppl.):17–23.

TWOMEY, A. C. 1936. Climographic studies of certain introduced and migratory birds. Ecology 17:122–132.

VAN DER MEER, J., and T. PIERSMA. 1994. Physiologically inspired regression models for estimating and predicting nutrient stores and their composition in birds. Physiol. Zool. 67:305–329.

VERBOVEN, N., and T. PIERSMA. 1995. Is the evaporative water loss of knot *Calidris canutus* higher in tropical than in temperate climates? Ibis 137:308–316.

WALLGREN, H. 1954. Energy metabolism of two species of the genus *Emberiza* as correlated with distributions and migration. Acta Zool. Fenn. 84:1–110.

WARKENTIN, I. G., and N. H. WEST. 1990. Impact of long-term captivity on basal metabolism in birds. Comp. Biochem. Physiol. 96A:379–381.

WEATHERS, W. W. 1979. Climatic adaptation in avian standard metabolic rate. Oecologia 42:81–89.

WEATHERS, W. W., D. L. WEATHERS, and C. VAN RIPER III. 1983. Basal metabolism of the Apapane: comparison of freshly caught birds with long-term captives. Auk 100: 977–978.

WEBSTER, A. J. F. 1981. The energetic efficiency of metabolism. Proc. Nutr. Soc. 40: 121–128.

WIERSMA, P., and T. PIERSMA. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of red knots. Condor 96:257–279.

WILKINSON, L. 1990. SYSTAT: the system for statistics. SYSTAT, Evanston, Ill.

WITHERS, P. C. 1977. Measurements of V_{O_2}, V_{CO_2} and evaporative water loss with a flow-through mask. J. Appl. Physiol. 42:120–123.

WITHERS, P. C., and J. B. WILLIAMS. 1990. Metabolic and respiratory physiology of an arid adapted Australian bird, the spinifex pigeon. Condor 92:961–969.